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Research Article

Dynamics of Planar Systems That Model Stage-Structured Populations

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We study a general discrete planar system for modeling stage-structured populations. Our results include conditions for the global convergence of orbits to zero (extinction) when the parameters (vital rates) are time and density dependent. When the parameters are periodic we obtain weaker conditions for extinction. We also study a rational special case of the system for Beverton-Holt type interactions and show that the persistence equilibrium (in the positive quadrant) may be globally attracting even in the presence of interstage competition. However, we determine that with a sufficiently high level of competition, the persistence equilibrium becomes unstable (a saddle point) and the system exhibits period two oscillations.

1. Introduction

Stage-structured models of single-species populations with lowest dimension in discrete time are expressed as planar systems of difference equations. For a general expression of these models, consider system

$$A(t+1) = s_1(t)\,\sigma_1\left(c_{11}(t)\,J(t), c_{12}(t)\,A(t)\right)J(t) + s_2(t)\,\sigma_2\left(c_{21}(t)\,J(t), c_{22}(t)\,A(t)\right)A(t), \tag{1a}$$

$$J(t+1) = b(t)\,\phi\left(c_1(t)\,J(t), c_2(t)\,A(t)\right)A(t) \tag{1b}$$

from [1] in which $J(t)$ and $A(t)$ are numbers (or densities) of juveniles and adults, respectively, remaining after t (juvenile) periods. The vital rates s_i and b (survival and inherent low density fertility) as well as the competition coefficients c_i and c_{ij} in (1a) and (1b) may be density dependent; that is, they may depend on J and A and also explicitly on time; that is, the system may be nonautonomous. Early examples of matrix models used in species populations dynamics can be found in [2–5] and their comprehensive treatment is provided in [6].

Under certain constraints on the various functions, including periodic vital rates and competition coefficients having the same common period p, sufficient conditions for global convergence to zero (extinction) as well as the existence of periodic orbits for (1a) and (1b) are established in [1]. If μ is the mean fertility rate (the mean value of $b(t)$ above), then it is also shown that orbits of period p appear when μ exceeds a critical value μ_c, while global convergence to 0 or extinction occurs when $\mu < \mu_c$. On the other hand, conditions under which the species survives (i.e. *permanence*) were studied in [7, 8].

In this paper, we study the following abstraction of the matrix model (1a) and (1b):

$$x_{n+1} = \sigma_{1,n}\left(x_n, y_n\right)y_n + \sigma_{2,n}\left(x_n, y_n\right)x_n, \tag{2a}$$

$$y_{n+1} = \phi_n\left(x_n, y_n\right)x_n, \tag{2b}$$

where for each time period $n \geq 0$ the functions $\sigma_{1,n}, \sigma_{2,n}, \phi_n : [0,\infty)^2 \rightarrow [0,\infty)$ are bounded on the compact sets in $[0,\infty)^2$. This feature allows for $(0,0)$ to be a fixed point of the system and it is true if, for example, $\sigma_{1,n}, \sigma_{2,n}, \phi_n$ are continuous functions for every n. Under biological constraints on the parameters, we may think of $x_n = A(n)$ and $y_n = J(n)$ as in (1a) and (1b).

System (2a) and (2b) includes typical stage-structured models in the literature. For instance, the tadpole-adult model for the green tree frog *Hyla cinerea* population that is proposed in [9] may be expressed as

$$x_n = \frac{y_n}{a + k_1 y_n} + \frac{x_n}{c + k_2 x_n}, \tag{3a}$$

$$y_n = b_n x_n. \tag{3b}$$

This is a system of type (2a) and (2b) with Beverton-Holt type functions σ_1 and σ_2. Competition in (3a) and (3b) occurs separately among juveniles and adults but not between the two classes, as they feed on separate resources; thus σ_1 and σ_2 do not depend on both juvenile and adult numbers and ϕ is independent of both numbers. Two cases are analyzed in [9]: (i) continuous breeding with constant $b_n = b$ so that (3a) and (3b) is autonomous and (ii) seasonal breeding where b_n is periodic. In addition to considering extinction and survival in the autonomous case, it is shown that seasonal breeding may be deleterious (relative to continuous breeding) for populations with high birth rates, but it can be beneficial with low birth rates.

Another system of type (2a) and (2b) is the autonomous stage-structured model with harvesting that is discussed in [10, 11], which may be written as

$$x_{n+1} = \left(1 - h_j\right) s_j y_n + \left(1 - h_a\right) s_a x_n, \tag{4a}$$

$$y_{n+1} = x_n f\left(\left(1 - h_a\right) x_n\right). \tag{4b}$$

The numbers $h_j, h_a \in [0, 1]$ denote the harvest rates of juveniles and adults, respectively. The stock-recruitment function $f : [0, \infty) \rightarrow [0, \infty)$ may be compensatory (e.g., Beverton-Holt [12]) or overcompensatory (e.g., Ricker [13]). Compensatory recruitment is used in populations where recruitment increases with increase in densities before reaching an asymptote, while in overcompensatory models recruitment declines as density increases (see [11, 14]). A thorough analysis of the dynamics of (4a) and (4b) with the Ricker function appears in [10]. The results in [10, 11] clarify many issues with regard to the effects of harvesting in stage-structured models such as global convergence to 0 and the existence of a stable survival equilibrium as well as the so-called *hydra effect* for different harvesting scenarios and with different recruitment functions; this refers to the counter-intuitive situation where an increase in the harvest or mortality rate results in a corresponding increase in the total population; for example, see [15–17].

Also studied in [10] is the occurrence of periodic and nonperiodic attractors and chaotic behavior for certain parameter ranges.

Next, the model in [18] studies the harvesting and predation of sex- and age-structured populations. Although the added stage for two sexes results in a three-dimensional model, the existence of an attracting, invariant planar manifold reduces the study of the asymptotics of the system to that of the planar system:

$$x_{n+1} = p s_Y y_n + s x_n, \tag{5a}$$

$$y_{n+1} = x_n f\left(y_n + \frac{x_n}{p}\right), \tag{5b}$$

where the density-dependent per capita reproductive rate f may be Beverton-Holt or Ricker similarly to f in (4b). Here x_n is the number of females and y_n is the number of young members in the population (the male population is a fixed proportion of the females).

We also mention the adult-juvenile model

$$x_{n+1} = s_1 y_n, \tag{6a}$$

$$y_{n+1} = x_n f\left(x_n, y_n\right) \tag{6b}$$

in which all adults are removed through harvesting, predation, migration, or just dying after one period, as in the case of semelparous species, that is, an organism that reproduces only once before death. In [19] conditions for the global attractivity of the positive fixed point and the occurrence of two cycles for (6a) and (6b) are obtained. A significant difference between (5a), (5b), (6a), and (6b) and systems (3a), (3b), (4a), and (4b) is the fact that y_{n+1} in (5b) or in (6b) may depend on both x_n and y_n.

We study the qualitative properties of the orbits of (2a) and (2b) such as uniform boundedness and global convergence to 0 under minimal restrictions on time-dependent parameters. Biological constraints may be readily imposed to obtain special cases relevant to population models.

We also investigate convergence to zero with periodic parameters (extinction in a periodic environment). In particular, we show that convergence to zero occurs even if the mean value of $\sigma_{2,n}$ exceeds 1, a situation that cannot occur if $\sigma_{2,n}$ is constant in n; see Remark 16 below.

In the final section we study the dynamics of a rational special case of (2a) and (2b). Sufficient conditions for the global asymptotic stability of a fixed point in the positive quadrant $[0, \infty)^2$ as well as conditions for the occurrence of orbits of prime period two are obtained. In particular, we establish that a sufficiently high level of interspecies competition tends to destabilize the survival fixed point and result in periodic oscillations.

Discrete population models generally have been studied by numerous authors; see, for example, [20–32] and the references therein.

2. Uniform Boundedness of Orbits

Conditions under which the orbits of (2a) and (2b) are bounded are not transparent. In this section we obtain general results about the uniform boundedness of orbits of (2a) and (2b) in the positive quadrant $[0, \infty)^2$. We begin with a simple, yet useful lemma.

Lemma 1. *Let $\alpha > 0$, let $0 < \beta < 1$, and let $x_0 \geq 0$. If for all $n \geq 0$*

$$x_{n+1} \leq \alpha + \beta x_n \tag{7}$$

then for every $\varepsilon > 0$ and all sufficiently large values of n

$$x_n \leq \frac{\alpha}{1 - \beta} + \varepsilon. \tag{8}$$

Proof. Let $u_0 = x_0$ and note that every solution of the linear, first-order equation $u_{n+1} = \alpha + \beta u_n$ converges to its fixed point $\alpha/(1-\beta)$. Furthermore,

$$\begin{aligned} x_1 &\leq \alpha + \beta x_0 = \alpha + \beta u_0 = u_1, \\ x_2 &\leq \alpha + \beta x_1 \leq \alpha + \beta u_1 = u_2 \end{aligned} \tag{9}$$

and, by induction, $x_n \leq u_n$. Since $u_n \to \alpha/(1-\beta)$ for every $\varepsilon > 0$ and all sufficiently large n,

$$x_n \leq u_n \leq \frac{\alpha}{1-\beta} + \varepsilon. \tag{10}$$

□

Theorem 2. *Let $\sigma_{1,n}$, $\sigma_{2,n}$, ϕ_n be bounded on the compact sets in $[0,\infty)^2$ for each $n = 0, 1, 2, \ldots$ and suppose that for some $r, M > 0$*

$$\sup_{(u,v)\in[0,r]^2} \sigma_{2,n}(u,v) \leq M \quad \forall n \geq 0; \tag{11}$$

that is, the sequence of functions $\{\sigma_{2,n}\}$ is uniformly bounded on the square $[0,r]^2$. If there are numbers $M_0, M_1 > 0$ and $\overline{\sigma} \in (0,1)$ such that uniformly for all n

$$u\phi_n(u,v) \leq M_0 \quad \text{if } (u,v) \in [0,\infty)^2, \tag{12}$$

$$\sigma_{1,n}(u,v) \leq M_1 \quad \text{if } (u,v) \in [0,\infty) \times [0, M_0], \tag{13}$$

$$\sigma_{2,n}(u,v) \leq \overline{\sigma} \quad \text{if } (u,v) \in (r,\infty) \times [0, M_0], \tag{14}$$

then all orbits of (2a) and (2b) are uniformly bounded and for all sufficiently large values of n satisfy

$$\begin{aligned} 0 \leq x_n &\leq \frac{M_0 M_1 + rM + \overline{\sigma}}{1-\overline{\sigma}}, \\ y_n &\leq M_0. \end{aligned} \tag{15}$$

Proof. By (2b) and (12) $y_n \leq M_0$ for $n \geq 1$ so by (2a) and (13)

$$0 \leq x_{n+1} \leq M_0 M_1 + \sigma_{2,n}(u,v)\, x_n. \tag{16}$$

By (11) and (14)

$$\begin{aligned} 0 \leq x_{n+1} &\leq M_0 M_1 + \max\{\overline{\sigma} x_n, Mr\} \\ &\leq \overline{\sigma} x_n + M_0 M_1 + rM. \end{aligned} \tag{17}$$

Next, applying Lemma 1 with $\varepsilon = \overline{\sigma}/(1-\overline{\sigma})$, we obtain for all (large) n

$$0 \leq x_n \leq \frac{M_0 M_1 + rM}{1-\overline{\sigma}} + \varepsilon = \frac{M_0 M_1 + rM + \overline{\sigma}}{1-\overline{\sigma}} \tag{18}$$

as stated. □

Corollary 3. *For functions $\sigma_{1,n}$, $\sigma_{2,n}$, ϕ_n defined on $[0,\infty)^2$ for $n = 0, 1, 2, \ldots$ assume that there are numbers $M_0, M_1 > 0$ and $\overline{\sigma} \in (0,1)$ such that for all $(u,v) \in [0,\infty)^2$ and all n*

$$\begin{aligned} u\phi_n(u,v) &\leq M_0, \\ \sigma_{1,n}(u,v) &\leq M_1, \\ \sigma_{2,n}(u,v) &\leq \overline{\sigma}. \end{aligned} \tag{19}$$

Then all orbits of (2a) and (2b) are uniformly bounded and for all sufficiently large values of n

$$\begin{aligned} 0 \leq x_n &\leq \frac{M_0 M_1 + \overline{\sigma}}{1-\overline{\sigma}}, \\ y_n &\leq M_0. \end{aligned} \tag{20}$$

Theorem 2 is more general than the preceding corollary. For instance, Corollary 3 does not apply to system

$$\begin{aligned} x_{n+1} &= a x_n + \frac{b y_n^2}{1 + c x_n}, \\ y_{n+1} &= \frac{\alpha x_n}{1 + \beta x_n + \gamma y_n}. \end{aligned} \tag{21}$$

However, if $a \in (0,1)$, $b, \alpha, \beta > 0$, and $c, \gamma \geq 0$, then all orbits of this system with initial values in $[0,\infty)^2$ are uniformly bounded by Theorem 2.

3. Global Attractivity of the Origin

In this section we obtain general sufficient conditions for the convergence of all orbits of the system to $(0,0)$. For population models these yield conditions that imply the extinction of species.

3.1. General Results. We start with the following lemma; see [33] for the proof and some background on this result.

Lemma 4. *Let $\alpha \in (0,1)$ and assume that the functions $f_n : [0,\infty)^{k+1} \to [0,\infty)$ satisfy the inequality*

$$f_n(u_0, \ldots, u_k) \leq \alpha \max\{u_0, \ldots, u_k\} \tag{22}$$

for all $(u_0, \ldots, u_k) \in [0,\infty)$ and all $n \geq 0$. Then for every solution $\{x_n\}$ of the difference equation

$$x_{n+1} = f_n(x_n, x_{n-1}, \ldots, x_{n-k}) \tag{23}$$

the following is true:

$$x_n \leq \alpha^{n/(k+1)} \max\{x_0, x_{-1}, \ldots, x_{-k}\}. \tag{24}$$

Note that (22) implies that $x_n = 0$ is a constant solution of (23) and furthermore (24) implies that this solution is globally exponentially stable.

Throughout this section we assume that $\sigma_{i,n}$, ϕ_n are all bounded functions for $i = 1, 2$ and every $n = 0, 1, 2, \ldots$. Then the following are well-defined sequences of real numbers:

$$\begin{aligned} \overline{\sigma}_{i,n} &= \sup_{u,v\geq 0} \sigma_{i,n}(u,v), \\ \overline{\phi}_n &= \sup_{u,v\geq 0} \phi_n(u,v). \end{aligned} \tag{25}$$

Theorem 5. *If the inequality*

$$\limsup_{n\to\infty} \left(\overline{\sigma}_{1,n}\overline{\phi}_{n-1} + \overline{\sigma}_{2,n}\right) < 1 \tag{26}$$

holds, then $\lim_{n\to\infty} x_n = 0$ *for every orbit* $\{(x_n, y_n)\}$ *of the planar system (2a) and (2b) in the positive quadrant* $[0,\infty)^2$. *If also either the sequence* $\{\overline{\phi}_n\}$ *is bounded or the inequality*

$$\liminf_{n\to\infty} \overline{\sigma}_{1,n} > 0, \tag{27}$$

holds, then every orbit of (2a) and (2b) converges to $(0,0)$.

Proof. By (26) there is $\delta \in (0,1)$ such that $\overline{\sigma}_{1,n}\overline{\phi}_{n-1} + \overline{\sigma}_{2,n} \le \delta$ for all (large) n. From (2a)

$$y_n \le \overline{\phi}_{n-1} x_{n-1} \tag{28}$$

so for all (large) n (2b) yields

$$\begin{aligned} x_{n+1} &\le \overline{\phi}_{n-1}\overline{\sigma}_{1,n} x_{n-1} + \overline{\sigma}_{2,n} x_n \\ &\le \left(\overline{\sigma}_{1,n}\overline{\phi}_{n-1} + \overline{\sigma}_{2,n}\right) \max\{x_n, x_{n-1}\} \\ &\le \delta \max\{x_n, x_{n-1}\}. \end{aligned} \tag{29}$$

Lemma 4 now implies that $\lim_{n\to\infty} x_n = 0$. Furthermore either by hypothesis there is a positive number μ such that $\overline{\phi}_n \le \mu$ or by (27) there is a positive number ρ such that $\overline{\sigma}_{1,n} \ge \rho$ for all (large) n so that

$$\overline{\phi}_{n-1} \le \frac{\delta - \overline{\sigma}_{2,n}}{\overline{\sigma}_{1,n}} \le \frac{\delta}{\rho} \tag{30}$$

for all sufficiently large values of n. Now, if $M = \mu$ or $M = \delta/\rho$ as the case may be, then from (2b) in the planar system we see that

$$\lim_{n\to\infty} y_n \le \lim_{n\to\infty} \overline{\phi}_{n-1} x_{n-1} \le M \lim_{n\to\infty} x_{n-1} = 0 \tag{31}$$

and the proof is complete. □

Remark 6. (1) Theorem 5 is valid even if the separate sequences $\{\sigma_{1,n}\}$ or $\{\overline{\phi}_n\}$ are not bounded by 1 as long as for all n large enough $\overline{\sigma}_{1,n}\overline{\phi}_{n-1} \le \delta - \overline{\sigma}_{2,n}$.

(2) If (26) is satisfied but $\{\overline{\phi}_n\}$ is unbounded and $\{\overline{\sigma}_{1,n}\}$ does not satisfy (27) then y_n may not converge to 0; see the example following Corollary 18 below.

We consider an application of Theorem 5 to "noisy" autonomous system next. Let ε_n, $\varepsilon_{i,n}$, $i = 1, 2$, be bounded sequences of real numbers and let

$$\begin{aligned} \overline{\varepsilon} &= \sup_{n\ge 1} \varepsilon_n, \\ \overline{\varepsilon}_i &= \sup_{n\ge 1} \varepsilon_{i,n}, \quad i = 1, 2. \end{aligned} \tag{32}$$

Additionally, let $\sigma_1, \sigma_2, \phi : [0,\infty)^2 \to [0,\infty)$ be bounded functions and denote their supremums over $[0,\infty)^2$ by $\overline{\sigma}_1, \overline{\sigma}_2, \overline{\phi}$, respectively. If in (2a) and (2b) we have

$$\begin{aligned} \phi_n(x_n, y_n) &= \phi(x_n, y_n) + \varepsilon_n, \\ \sigma_{i,n}(x_n, y_n) &= \sigma_i(x_n, y_n) + \varepsilon_{i,n}, \quad i = 1, 2 \end{aligned} \tag{33}$$

then we refer to (2a) and (2b) as an autonomous system with low-amplitude disturbances or fluctuations in the rates σ_1, σ_2, ϕ, assuming that all three of these are positive functions and for all $u, v \ge 0$

$$\begin{aligned} |\overline{\varepsilon}| &\le \phi(u, v), \\ |\overline{\varepsilon}_i| &\le \sigma_i(u, v), \quad i = 1, 2. \end{aligned} \tag{34}$$

These inequalities ensure that the functions ϕ_n and $\sigma_{i,n}$ are positive, as required for (2a) and (2b).

Corollary 7. *Suppose that (2a) and (2b) is an autonomous system with low-amplitude disturbances or fluctuations in the above sense. If*

$$\left(\overline{\sigma}_1 + \overline{\varepsilon}_1\right)\left(\overline{\phi} + \overline{\varepsilon}\right) + \overline{\sigma}_2 + \overline{\varepsilon}_2 < 1 \tag{35}$$

then the origin is the unique, globally asymptotically stable fixed point of (2a) and (2b) relative to the positive quadrant $[0,\infty)$.

Note that (35) holds for nontrivial sequences ε_n, $\varepsilon_{i,n}$ of real numbers if $\overline{\sigma}_1\overline{\phi} + \overline{\sigma}_2 < 1$.

Remark 8. Since in the above discussion the sequences ϵ_n, $\epsilon_{i,n}$, $i = 1, 2$, are arbitrary bounded sequences, they can also be sequences of random variables that are drawn from distributions with finite support. For example, ϵ_n, $\epsilon_{i,n}$ can be drawn from uniform distribution on some interval $[0,\theta]$ so long as

$$\left(\overline{\sigma}_1 + \theta\right)\left(\overline{\phi} + \theta\right) + \overline{\sigma}_2 + \theta < 1. \tag{36}$$

Corollary 7 will hold, implying that the origin is globally attracting even in the presence of noise.

In the autonomous case where the three parameter functions $\sigma_{1,n}$, $\sigma_{2,n}$, ϕ_n do not depend on n at all, we have the following planar system:

$$x_{n+1} = \sigma_1(x_n, y_n)\, y_n + \sigma_2(x_n, y_n)\, x_n, \tag{37a}$$

$$y_{n+1} = \phi(x_n, y_n)\, x_n. \tag{37b}$$

If in Corollary 7 we set $\overline{\varepsilon}_i, \overline{\varepsilon} = 0$ in (35) then we obtain the following result for the above autonomous system.

Corollary 9. *Assume that* $\sigma_1, \sigma_2, \phi : [0,\infty)^2 \to [0,\infty)$ *are bounded functions and the following inequality holds:*

$$\overline{\sigma}_1\overline{\phi} + \overline{\sigma}_2 < 1; \tag{38}$$

then the origin is the unique, globally asymptotically stable fixed point of (37a) and (37b) relative to the positive quadrant $[0,\infty)^2$.

Inequality (38) may be explicitly related to the local asymptotic stability of the origin for (37a) and (37b) when the functions σ_1, σ_2, ϕ are smooth. Consider the associated mapping

$$F(u, v) = \left(u\sigma(u, v) + v\sigma_1(u, v),\, u\phi(u, v)\right) \tag{39}$$

whose linearization at $(0,0)$ has eigenvalues

$$\lambda^{\pm}=\frac{\sigma_2(0,0)\pm\sqrt{\sigma_2(0,0)^2+4\sigma_1(0,0)\phi(0,0)}}{2}. \tag{40}$$

These are real and a routine calculation shows that $|\lambda^{\pm}|<1$ if

$$\sigma_1(0,0)\phi(0,0)+\sigma_2(0,0)<1. \tag{41}$$

Under suitable differentiability hypotheses, this inequality is implied by (38) and is equivalent to it if the suprema of σ_2 and $\sigma_1\phi$ occur at $(0,0)$.

3.2. Folding the System. In the next and later sections it will be convenient to fold system (2a) and (2b) to a second-order equation; see [34] for more details on folding. System (2a) and (2b) in general folds as follows: substitute for y_{n+1} from (2b) into (2a) to obtain

$$\begin{aligned}x_{n+2}&=\sigma_{1,n+1}\left(x_{n+1},\phi_n\left(x_n,h_n\left(x_n,x_{n+1}\right)\right)x_n\right)\\&\quad\cdot\phi_n\left(x_n,h_n\left(x_n,x_{n+1}\right)\right)x_n\\&\quad+\sigma_{2,n+1}\left(x_{n+1},\phi_n\left(x_n,h_n\left(x_n,x_{n+1}\right)\right)x_n\right)x_{n+1},\end{aligned} \tag{42}$$

where

$$h_n\left(x_n,x_{n+1}\right)=y_n \tag{43}$$

is derived by solving (2a) for y_n. Although an explicit formula for h_n is not feasible in general, it is readily obtained in typical cases; for instance, suppose that $\sigma_{2,n}(u,v)=\sigma_{2,n}(u)$ and $\sigma_{1,n}(u,v)=\sigma_{1,n}(u)$ are both independent of (or constant in) v for all n; note that systems (3a), (3b), (4a), (4b), (5a), (5b), (6a), and (6b) are all of this type. In this case it is clear that

$$y_n=h_n\left(x_n,x_{n+1}\right)=\frac{x_{n+1}-\sigma_{2,n}\left(x_n\right)x_n}{\sigma_{1,n}\left(x_n\right)} \tag{44}$$

and furthermore (42) reduces to

$$\begin{aligned}x_{n+2}&=\sigma_{1,n+1}\left(x_{n+1}\right)\phi_n\left(x_n,\frac{x_{n+1}-\sigma_{2,n}\left(x_n\right)x_n}{\sigma_{1,n}\left(x_n\right)}\right)x_n\\&\quad+\sigma_{2,n+1}\left(x_{n+1}\right)x_{n+1}.\end{aligned} \tag{45}$$

The pair of first-order equations (44) and (45) represents folding of (2a) and (2b). Note that with positive parameter functions, each pair $x_0,y_0\geq 0$ generates an orbit $\{(x_n,y_n)\}$ of (2a) and (2b) that is in $[0,\infty)^2$ for all n. So we have $x_{n+1},x_n\geq 0$ and also by (43) $h_n(x_n,x_{n+1})\geq 0$ so $\phi_n(x_n,h_n(x_n,x_{n+1}))$ is well defined for every such orbit of (2a) and (2b).

Remark 10. An even simpler reduction than the above is possible if $\phi_n(u,v)=\phi_n(u)$ is independent of (or constant in) v. In this case,

$$\begin{aligned}x_{n+2}&=\sigma_{1,n+1}\left(x_{n+1},\phi_n\left(x_n\right)x_n\right)\phi_n\left(x_n\right)x_n\\&\quad+\sigma_{2,n+1}\left(x_{n+1},\phi_n\left(x_n\right)x_n\right)x_{n+1}\end{aligned} \tag{46}$$

and it is not necessary to solve (2a) for y_n implicitly (i.e., the system folds without inversions). Special cases of this type include systems (3a), (3b), (4a), and (4b).

3.3. Global Convergence to Zero with Periodic Parameters. The results in this section show that global convergence to zero may occur even if (26) does not hold; see Remark 16 below. Recall from the proof of Theorem 5 that

$$x_{n+1}\leq\sigma_{1,n}\overline{\phi}_{n-1}x_{n-1}+\overline{\sigma}_{2,n}x_n. \tag{47}$$

The right-hand side of the above inequality is a linear expression. Consider the linear difference equation

$$\begin{aligned}u_{n+1}&=a_nu_n+b_nu_{n-1},\\a_{n+p_1}&=a_n,\\b_{n+p_2}&=b_n,\end{aligned} \tag{48}$$

where the coefficients a_n and b_n are nonnegative and their periods p_1 and p_2 are positive integers with least common multiple $p=\operatorname{lcm}(p_1,p_2)$; we say that the linear difference equation (48) is periodic with period p. In this study we assume that

$$a_n,b_n\geq 0,\quad n=0,1,2,\ldots. \tag{49}$$

By Lemma 4 every solution of (48) converges to zero if $a_n+b_n<1$ for all n. However, it is known that convergence to zero may occur even when a_n+b_n exceeds 1 (for infinitely many n in the periodic case). We use the approach in [35] to examine the consequences of this issue when the planar system has periodic parameters. The following result is an immediate consequence of Theorem 13 in [35].

Lemma 11. *Assume that α_j, β_j for $j=1,2,\ldots,p$ are obtained by iteration from (48) from the real initial values:*

$$\begin{aligned}\alpha_0&=0,\\\alpha_1&=1;\\\beta_0&=1,\\\beta_1&=0.\end{aligned} \tag{50}$$

Suppose that the quadratic polynomial

$$\alpha_pr^2+\left(\beta_p-\alpha_{p+1}\right)r-\beta_{p+1}=0 \tag{51}$$

is proper, that is, not $0=0$, and suppose that it has a real root $r_1\neq 0$. If the recurrence

$$r_{n+1}=a_n+\frac{b_n}{r_n} \tag{52}$$

generates nonzero real numbers $r_2,\ldots,r_p$ then $\{r_n\}_{n=1}^{\infty}$ is periodic with preiod p and yields a triangular system of first-order equations that is equivalent to (48) as follows:

$$\begin{aligned}t_{n+1}&=-\frac{b_n}{r_n}t_n,\\t_1&=u_1-r_1u_0,\end{aligned} \tag{53}$$

$$u_{n+1}=r_{n+1}u_n+t_{n+1}. \tag{54}$$

System (53) and (54) is also known as a *semiconjugate factorization* of (48); see [36] for an introduction to this concept. The sequence $\{r_n\}$ that is generated by (52) is said to be *(unitary) eigensequence* of (48). Eigenvalues are essentially constant eigensequences for if $p = 1$ in Lemma 11 then (51) reduces to

$$\alpha_1 r^2 + (\beta_1 - \alpha_2) r - \beta_2 = 0,$$
$$r^2 - a_1 r - b_1 = 0 \tag{55}$$

and the latter equation is the standard characteristic equation of (48) with constant coefficients; see [35] for more details on the semiconjugate factorization of linear difference equations.

Each of (53) and (54) readily yields a solution by iteration as follows:

$$t_n = t_1 (-1)^{n-1} \left(\frac{b_1 b_2 \cdots b_{n-1}}{r_1 r_2 \cdots r_{n-1}} \right), \tag{56}$$

$$\begin{aligned} u_n &= r_n r_{n-1} \cdots r_2 u_1 + r_n r_{n-1} \cdots r_3 t_2 + \cdots r_n t_{n-1} + t_n \\ &= r_n r_{n-1} \cdots r_2 r_1 u_0 + \sum_{i=1}^{n-1} r_n r_{n-1} \cdots r_{i+1} t_i + t_n. \end{aligned} \tag{57}$$

Lemma 12. *Suppose that the numbers α_n and β_n are defined as in Lemma 11, though we do not assume that (48) is periodic here. Then*

(a) *$\beta_n = 0$ for all $n \geq 2$ if and only if $b_1 = 0$;*

(b) *if (49) holds then for all $n \geq 2$*

$$\begin{aligned} \alpha_n &\geq a_1 a_2 \cdots a_{n-1}, \\ \beta_n &\geq b_1 a_2 \cdots a_{n-1}, \end{aligned} \tag{58}$$

$$\begin{aligned} \alpha_{2n-1} &\geq b_2 b_4 \cdots b_{2n-2}, \\ \beta_{2n} &\geq b_1 b_3 \cdots b_{2n-1}. \end{aligned} \tag{59}$$

Proof. (a) Let $b_1 = 0$. Then $\beta_2 = b_1 = 0$ and since $\beta_1 = 0$ by definition it follows that $\beta_3 = 0$. Induction completes the proof that $\beta_n = 0$ if $n \geq 2$. The converse is obvious since $b_1 = \beta_2$.

(b) Since $\alpha_2 = a_1$ and $\beta_2 = b_1$ the stated inequalities hold for $n = 2$. If (58) is true for some $k \geq 2$ then

$$\begin{aligned} \alpha_{k+1} &= a_k \alpha_k + b_k \alpha_{k-1} \geq a_k \alpha_k \geq a_1 a_2 \cdots a_{k-1} a_k, \\ \beta_{k+1} &= a_k \beta_k + b_k \beta_{k-1} \geq a_k \beta_k \geq b_1 a_2 \cdots a_{k-1} a_k. \end{aligned} \tag{60}$$

Now, the proof is completed by induction. The proof of (59) is similar since

$$\begin{aligned} \alpha_3 &= a_2 \alpha_2 + b_2 \alpha_1 \geq b_2, \\ \beta_4 &= a_3 \beta_3 + b_3 \beta_2 \geq b_3 b_1 \end{aligned} \tag{61}$$

and if (59) holds for some $k \geq 2$ then

$$\begin{aligned} \alpha_{2k+1} &\geq b_{2k} \alpha_{2k-1} \geq b_2 b_4 \cdots b_{2k-2} b_{2k}, \\ \beta_{2k+2} &\geq b_{2k+1} \beta_{2k} \geq b_1 b_3 \cdots b_{2k-1} b_{2k+1} \end{aligned} \tag{62}$$

which establishes the induction step. □

Lemma 13. *Assume that (49) holds with $a_i > 0$ for $i = 1, \ldots, p$ and (48) is periodic with period $p \geq 2$. Then one has the following.*

(a) Equation (48) has a positive (hence unitary) eigensequence $\{r_n\}$ of period p.

(b) If $b_i > 0$ for $i = 1, \ldots, p$ then

$$\begin{aligned} & r_1 r_2 \cdots r_p \\ & = \frac{1}{2} \left(\alpha_{p+1} + \beta_p + \sqrt{\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1}} \right). \end{aligned} \tag{63}$$

Hence, $r_1 r_2 \cdots r_p < 1$ if

$$\alpha_p \beta_{p+1} < \left(1 - \alpha_{p+1}\right)\left(1 - \beta_p\right). \tag{64}$$

(c) If $b_i < 1$ for $i = 1, \ldots, p$ then $r_1 r_2 \cdots r_p > b_1 b_2 \cdots b_p$.

Proof. (a) Lemma 12 shows that $\alpha_i > 0$ for $i = 2, \ldots, p + 1$. Now, either (i) $b_1 > 0$ or (ii) $b_1 = 0$. In case (i), the root r^+ of the quadratic polynomial (51) is positive since by Lemma 12 $\beta_{p+1} > 0$ and thus

$$\begin{aligned} r^+ &= \frac{\alpha_{p+1} - \beta_p + \sqrt{\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1}}}{2\alpha_p} \\ &> \frac{\alpha_{p+1} - \beta_p + \left|\alpha_{p+1} - \beta_p\right|}{2\alpha_p} \geq 0. \end{aligned} \tag{65}$$

If $r_1 = r^+$ then from (52) $r_i = a_{i-1} + b_{i-1}/r_{i-1} \geq a_{i-1} > 0$ for $i = 2, \ldots, p + 1$. Thus, by Lemma 11, (48) has a unitary (in fact positive) eigensequence of period p. If $b_1 = 0$ then by Lemma 12 $\beta_p = \beta_{p+1} = 0$ and (51) reduces to

$$\alpha_p r^2 - \alpha_{p+1} r = 0 \tag{66}$$

which has a root $r^+ = \alpha_{p+1}/\alpha_p > 0$. As in the previous case it follows that (48) has a positive eigensequence of period p.

(b) To establish (63), let $r_1 = r^+$ and note that (51) can be written as

$$r_1 = \frac{\alpha_{p+1} r_1 + \beta_{p+1}}{\alpha_p r_1 + \beta_p}. \tag{67}$$

Since $\{r_n\}$ has period p, $r_{p+1} = r_1$ so from (52) and the definition of the numbers α_n and β_n it follows that

$$\begin{aligned} a_p + \frac{b_p}{r_p} = r_{p+1} &= \frac{\alpha_{p+1} r_1 + \beta_{p+1}}{\alpha_p r_1 + \beta_p} \\ &= \frac{\left(a_p \alpha_p + b_p \alpha_{p-1}\right) r_1 + a_p \beta_p + b_p \beta_{p-1}}{\alpha_p r_1 + \beta_p} \\ &= \frac{a_p \left(\alpha_p r_1 + \beta_p\right) + b_p \left(\alpha_{p-1} r_1 + \beta_{p-1}\right)}{\alpha_p r_1 + \beta_p} \\ &= a_p + \frac{b_p}{\left(\alpha_p r_1 + \beta_p\right) / \left(\alpha_{p-1} r_1 + \beta_{p-1}\right)}. \end{aligned} \tag{68}$$

Since $b_p \neq 0$ it follows that

$$r_p = \frac{\alpha_p r_1 + \beta_p}{\alpha_{p-1} r_1 + \beta_{p-1}}. \quad (69)$$

We claim that if $b_i \neq 0$ for $i = 1, \ldots, p$ then

$$r_{p-j} = \frac{\alpha_{p-j} r_1 + \beta_{p-j}}{\alpha_{p-j-1} r_1 + \beta_{p-j-1}}, \quad j = 0, 1, \ldots, p-2. \quad (70)$$

This claim is easily seen to be true by induction; we showed that it is true for $j = 0$ and if (70) holds for some j then by (52)

$$\begin{aligned} a_{p-j-1} + \frac{b_{p-j-1}}{r_{p-j-1}} = r_{p-j} &= \frac{\left(a_{p-j-1}\alpha_{p-j-1} + b_{p-j-1}\alpha_{p-j-2}\right) r_1 + \left(a_{p-j-1}\beta_{p-j-1} + b_{p-j-1}\beta_{p-j-2}\right)}{\alpha_{p-j-1} r_1 + \beta_{p-j-1}} \\ &= \frac{a_{p-j-1}\left(\alpha_{p-j-1} r_1 + \beta_{p-j-1}\right) + b_{p-j-1}\left(\alpha_{p-j-2} r_1 + \beta_{p-j-2}\right)}{\alpha_{p-j-1} r_1 + \beta_{p-j-1}} = a_{p-j-1} + \frac{b_{p-j-1}\left(\alpha_{p-j-2} r_1 + \beta_{p-j-2}\right)}{\alpha_{p-j-1} r_1 + \beta_{p-j-1}} \end{aligned} \quad (71)$$

from which it follows that

$$r_{p-j-1} = \frac{\alpha_{p-j-1} r_1 + \beta_{p-j-1}}{\alpha_{p-j-2} r_1 + \beta_{p-j-2}} \quad (72)$$

and the induction argument is complete. Now, using (70), we obtain

$$\begin{aligned} r_p r_{p-1} \cdots r_2 r_1 &= \frac{\alpha_p r_1 + \beta_p}{\alpha_{p-1} r_1 + \beta_{p-1}} \frac{\alpha_{p-1} r_1 + \beta_{p-1}}{\alpha_{p-2} r_1 + \beta_{p-2}} \cdots \frac{\alpha_2 r_1 + \beta_2}{\alpha_1 r_1 + \beta_1} r_1 \\ &= \alpha_p r_1 + \beta_p. \end{aligned} \quad (73)$$

Given that $r_1 = r^+$ (73) implies that

$$\begin{aligned} r_1 r_2 \cdots r_p &= \alpha_p \frac{\alpha_{p+1} - \beta_p + \sqrt{\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1}}}{2\alpha_p} + \beta_p \\ &= \frac{1}{2}\left(\alpha_{p+1} + \beta_p + \sqrt{\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1}}\right) \end{aligned} \quad (74)$$

and (63) is obtained. Hence, $r_1 r_2 \cdots r_p < 1$ if

$$\alpha_{p+1} + \beta_p + \sqrt{\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1}} < 2. \quad (75)$$

Upon rearranging terms and squaring,

$$\begin{aligned} &\left(\alpha_{p+1} - \beta_p\right)^2 + 4\alpha_p \beta_{p+1} \\ &\quad < 4 - 4\left(\alpha_{p+1} + \beta_p\right) + \left(\alpha_{p+1} + \beta_p\right)^2 \end{aligned} \quad (76)$$

which reduces to (64) after straightforward algebraic manipulations.

(c) First, assume that p is odd. Then by (59)

$$\alpha_p \beta_{p+1} = \left(b_2 b_4 \cdots b_{p-1}\right)\left(b_1 b_3 \cdots b_p\right) = b_1 b_2 \cdots b_p \quad (77)$$

so from (63)

$$r_1 r_2 \cdots r_p > \sqrt{\alpha_p \beta_{p+1}} = \sqrt{b_1 b_2 \cdots b_p}. \quad (78)$$

If $b_i < 1$ for $i = 1, \ldots, p$ then $b_1 b_2 \cdots b_p < 1$ so $\sqrt{b_1 b_2 \cdots b_p} > b_1 b_2 \cdots b_p$ as required. Now let p be even. Then from (63) and (59)

$$r_1 r_2 \cdots r_p > \frac{\alpha_{p+1} + \beta_p}{2} \geq \frac{b_2 b_4 \cdots b_p + b_1 b_3 \cdots b_{p-1}}{2}. \quad (79)$$

If $b_i < 1$ for $i = 1, \ldots, p$ then $b_2 b_4 \cdots b_p \geq b_1 b_2 \cdots b_p$ and $b_1 b_3 \cdots b_{p-1} \geq b_1 b_2 \cdots b_p$ and the proof is complete. □

Some of the numbers a_i may exceed 1 in Lemma 13 without affecting the conclusions of the lemma. Additionally, not all the conditions in Lemma 13 are necessary. For instance, if $b_1 = 0$ then Lemma 13(c) holds trivially. Additionally, by Lemma 12(a), $\beta_n = 0$ for $n \geq 2$ so the following equality must hold instead of (63):

$$r_1 r_2 \cdots r_p = \alpha_{p+1}. \quad (80)$$

This is in fact true because $r_1 = r^+ = \alpha_{p+1}/\alpha_p$ so repeating the argument in the proof of Lemma 13(b) yields $r_{p-j} = \alpha_{p-j}/\alpha_{p-j-1}$ for $j = 0, 1, \ldots, p-2$. Hence

$$r_p r_{p-1} \cdots r_2 r_1 = \frac{\alpha_p}{\alpha_{p-1}} \frac{\alpha_{p-1}}{\alpha_{p-2}} \cdots \frac{\alpha_2}{\alpha_1} \frac{\alpha_{p+1}}{\alpha_p} = \alpha_{p+1} \quad (81)$$

as claimed. These observations establish the following version of Lemma 13.

Lemma 14. *Let $a_i > 0$ and let $b_i \geq 0$ for $i = 1, \ldots, p$ with $b_1 = 0$. Then the linear equation (48) has a positive (hence unitary) eigensequence $\{r_n\}$ of period p given by*

$$\begin{aligned} r_1 &= \frac{\alpha_{p+1}}{\alpha_p}, \\ r_j &= \frac{\alpha_j}{\alpha_{j-1}}, \quad j = 2, \ldots, p \end{aligned} \quad (82)$$

and $0 = b_1 b_2 \cdots b_p < r_1 r_2 \cdots r_p < 1$ if $\alpha_{p+1} < 1$.

In Lemma 14 some of the numbers a_i or b_i may exceed 1 without affecting the conclusions of the lemma.

Theorem 15. *Assume that (27) holds and the sequences and* $\{\overline{\sigma}_{1,n}\overline{\phi}_{n-1}\}$ *and* $\{\overline{\sigma}_{2,n}\}$ *have period p with* $\overline{\sigma}_{2,i} > 0$ *and* $\overline{\sigma}_{1,i}\overline{\phi}_{i-1} \geq 0$ *for* $i = 1, \ldots, p$. *Additionally let the numbers* α_n, β_n *be as previously defined with* $a_n = \overline{\sigma}_{2,n}$ *and* $b_n = \overline{\sigma}_{1,n}\overline{\phi}_{n-1}$. *All nonnegative orbits of the planar system converge to* $(0,0)$ *if either one of the following holds:*

(a) $0 < \overline{\sigma}_{1,i}\overline{\phi}_{i-1} < 1$ *and (64) holds.*

(b) $\overline{\sigma}_{1,1}\overline{\phi}_0 = 0$ *and* $\alpha_{p+1} < 1$.

Proof. Let $\{u_n\}$ be a solution of the linear equation (48) with $a_n = \overline{\sigma}_{2,n}$, $b_n = \overline{\sigma}_{1,n}\overline{\phi}_{n-1}$, $u_0 = x_0$, and $u_1 = x_1$. Then by (47)

$$x_2 \leq \overline{\sigma}_{1,1}\overline{\phi}_0 x_0 + \overline{\sigma}_{2,1}x_1 = \overline{\sigma}_{1,1}\overline{\phi}_0 u_0 + \overline{\sigma}_{2,1}u_1 = u_2,$$
$$x_3 \leq \overline{\sigma}_{1,2}\overline{\phi}_2 x_2 + \overline{\sigma}_{2,2}x_2 \leq \overline{\sigma}_{1,2}\overline{\phi}_1 u_1 + \overline{\sigma}_{2,2}u_2 = u_3. \quad (83)$$

By induction it follows that $x_n \leq u_n$. If (64) holds then, by Lemma 13, $\lim_{n\to\infty} u_n = 0$ so $\{x_n\}$ converges to 0. Furthermore, $\lim_{n\to\infty} y_n = 0$ as in the proof of Theorem 5 and the proof is complete. □

Remark 16. (1) Condition (64) involves the numbers α_j, β_j rather than the coefficients of (48) directly. In the case of period $p = 2$ the role of a_i and b_i is more apparent. Inequality (64) in this case is

$$\alpha_2\beta_3 < (1-\alpha_3)(1-\beta_2),$$
$$a_1a_2b_1 < (1-b_2-a_1a_2)(1-b_1) \quad (84)$$

and simple manipulations reduce the last inequality to

$$a_1a_2 < (1-b_1)(1-b_2). \quad (85)$$

(2) Inequality (85) holds even if $a_1 > 1$ or $a_2 > 1$ thus showing how global convergence to $(0,0)$ my occur when (26) does not hold. Furthermore, it is possible that (85) holds together with

$$\frac{a_1 + a_2}{2} > 1. \quad (86)$$

Note that (85) holds even with arbitrarily large mean value in (86) if say $a_1 \to 0$ as $a_2 \to \infty$. In population models this implies that if (85) holds with $a_n = \overline{\sigma}_{2,n}$ and $b_n = \overline{\sigma}_{1,n}\overline{\phi}_{n-1}$ then extinction may still occur after restocking the adult population to raise the mean value of the composite parameter $\overline{\sigma}_{2,n}$ above 1 by a wide margin.

(3) In Theorem 15 the individual sequences $\overline{\sigma}_{1,n}$, $\overline{\phi}_n$ need not be periodic or even bounded. Therefore, the theorem applies to (2a) and (2b) even if the system itself is not periodic as long as the combination $\overline{\sigma}_{1,n}\overline{\phi}_{n-1}$ of parameters is periodic along with $\overline{\sigma}_{2,n}$.

4. Dynamics of a Beverton-Holt Type Rational System

In this section we apply some of the preceding results and obtain some new ones to study boundedness, extinction, and modes of survival in some rational special cases of (2a) and (2b). In population models these types of systems include the Beverton-Holt type interactions. Specifically, we consider the following nonautonomous system and some of its special cases:

$$x_{n+1} = \frac{\alpha_{1,n}y_n}{1+\beta_{1,n}x_n+\gamma_{1,n}y_n} + \frac{\alpha_{2,n}x_n}{1+\beta_{2,n}x_n+\gamma_{2,n}y_n}, \quad (87a)$$

$$y_{n+1} = \frac{b_nx_n}{1+c_{1,n}x_n+c_{2,n}y_n}, \quad (87b)$$

where we assume that for all $n \geq 0$ and $i = 1, 2$

$$\alpha_{1,n} > 0,$$
$$b_n, \alpha_{2,n}, \beta_{i,n}, \gamma_{i,n}, c_{i,n} \geq 0 \quad (88)$$
$$b_n > 0 \text{ for infinitely many } n.$$

For example, if we think of α_i as the natural survival rates then the population model (3a) and (3b) is a special case of (87a) and (87b). If we allow α_i to include additional factors such as harvesting rates then (87a) and (87b) is an extension of the model in [11] (with a Beverton-Holt recruitment function) in the sense that the competition coefficients $\beta_{i,n}$, $\gamma_{i,n}$, and $c_{i,n}$ may be nonzero as well as time-dependent.

4.1. Uniform Boundedness and Extinction. We now examine boundedness and global convergence to 0 (extinction) in (87a) and (87b). The next result is in part a consequence of Corollary 3.

Corollary 17. *Assume that (88) holds.*

(a) Let the sequence $\{\alpha_{1,n}\}$ *be bounded and* $\limsup_{n\to\infty}\alpha_{2,n} < 1$. *If there is* $M_0 > 0$ *such that* $b_n \leq M_0c_{1,n}$ *for all n larger than a given positive integer then all orbits of (87a) and (87b) are uniformly bounded.*

(b) Let the sequence $\{b_n\}$ *be bounded and suppose that there is* $M > 0$ *such that*

$$\alpha_{1,n} \leq M\gamma_{1,n},$$
$$\alpha_{2,n} \leq M\beta_{2,n} \quad (89)$$

for all n larger than a given positive integer. Then all orbits of (87a) and (87b) are uniformly bounded.

Proof. (a) By hypothesis, for all (large) n,

$$\frac{b_nx_n}{1+c_{1,n}x_n+c_{2,n}y_n} \leq \frac{M_0c_{1,n}x_n}{1+c_{1,n}x_n+c_{2,n}y_n} < M_0. \quad (90)$$

Next, let

$$\sigma_{1,n}(u,v) = \frac{\alpha_{1,n}}{1+\beta_{1,n}u+\gamma_{1,n}v},$$
$$\sigma_{2,n}(u,v) = \frac{\alpha_{2,n}}{1+\beta_{2,n}u+\gamma_{2,n}v}. \quad (91)$$

By hypothesis, there is $M_1 > 0$ and $\delta \in (0,1)$ such that for all $u, v \geq 0$ and all sufficiently large values of n

$$\begin{aligned} \sigma_{1,n}(u,v) &\leq \alpha_{1,n} \leq M_1, \\ \sigma_{2,n}(u,v) &\leq \alpha_{2,n} \leq \delta. \end{aligned} \tag{92}$$

Now an application of Corollary 3 completes the proof of (a).

(b) By (89) for all large n it follows that

$$\frac{\alpha_{1,n} y_n}{1+\beta_{1,n}x_n+\gamma_{1,n}y_n} \leq \frac{M\gamma_{1,n}y_n}{1+\beta_{1,n}x_n+\gamma_{1,n}y_n} < M \tag{93}$$

and, likewise,

$$\frac{\alpha_{2,n} x_n}{1+\beta_{2,n}x_n+\gamma_{2,n}y_n} \leq \frac{M\beta_{2,n}x_n}{1+\beta_{2,n}x_n+\gamma_{2,n}y_n} < M \tag{94}$$

for all large n. Therefore, $x_n \leq 2M$. Next, if $\{b_n\}$ is bounded then $y_n \leq 2Mb_n$ is also bounded and the proof is complete. □

The next result follows readily from Theorem 5.

Corollary 18. *The origin* $(0,0)$ *attracts every orbit of (87a) and (87b) in* $[0,\infty)^2$ *if*

$$\limsup_{n\to\infty}\left(\alpha_{1,n}b_{n-1}+\alpha_{2,n}\right) < 1 \tag{95}$$

and either b_n *is bounded or* $\liminf_{n\to\infty}\alpha_{1,n} > 0$.

The above corollary is false when (95) holds if b_n is unbounded and thus $\alpha_{1,n}$ has a subsequence that converges to 0.

Example 19. Consider system

$$\begin{aligned} x_{n+1} &= \alpha^{-n}y_n + sx_n, \\ y_{n+1} &= \frac{\beta\alpha^n x_n}{1+cx_n}, \end{aligned} \tag{96}$$

where $\alpha > 1$, $\beta > 0$, $0 \leq s < 1$, $c \geq 0$, $\sigma_{1,n} = \alpha^{-n}$, and $b_n = \beta\alpha^n$. Then (95) is satisfied, so $\lim_{n\to\infty}x_n = 0$. But y_n does not approach 0 for large enough α; this may be inferred from Lemma 4 which shows that x_n converges to 0 at an exponential rate $\delta^{n/2}$ where $\delta = s+\beta/\alpha \in (0,1)$. Thus

$$y_n = \frac{1}{\alpha^{-n}}\left(x_{n+1}-sx_n\right) = \alpha^n\left(x_{n+1}-sx_n\right) \tag{97}$$

will not converge to 0 if α is sufficiently large.

Corollary 17 takes a simpler form for the autonomous special case of (87a) and (87b); namely,

$$x_{n+1} = \frac{\alpha_1 y_n}{1+\beta_1 x_n+\gamma_1 y_n} + \frac{\alpha_2 x_n}{1+\beta_2 x_n+\gamma_2 y_n}, \tag{98a}$$

$$y_{n+1} = \frac{bx_n}{1+c_1x_n+c_2y_n} \tag{98b}$$

with constant parameters

$$\begin{aligned} &\alpha_1, b > 0, \\ &\alpha_2, \beta_i, \gamma_i, c_i \geq 0. \end{aligned} \tag{99}$$

The following result is applicable to (3a) and (3b) as well as special cases of (4a), (4b), (5a), and (5b) with rational f.

Corollary 20. *Assume that (99) holds. All orbits of (98a) and (98b) in* $[0,\infty)^2$ *are uniformly bounded if either one of the following conditions holds:*

(a) $\alpha_2 < 1$ *and* $c_1 > 0$.

(b) $\gamma_1, \beta_2 > 0$.

It is noteworthy that if in part (a) above $c_1 = 0$ then (98a) and (98b) may have unbounded solutions as in, for example, system

$$\begin{aligned} x_{n+1} &= \alpha_1 y_n, \\ y_{n+1} &= \frac{bx_n}{1+c_2y_n}, \end{aligned} \tag{100}$$

where $\alpha_2 = c_1 = 0$ and the remaining parameters are positive. This system folds to the second-order rational equation

$$x_{n+2} = \frac{\alpha_1^2 b x_n}{\alpha_1 + c_2 x_{n+1}} \tag{101}$$

which is known to have unbounded solutions if $\alpha_1 b > 1$; see [37].

Corollary 18 likewise simplifies in the autonomous case.

Corollary 21. *Assume that (99) holds with* $\alpha_1 b + \alpha_2 < 1$. *Then the origin* $(0,0)$ *is the globally asymptotically stable fixed point of (98a) and (98b) relative to* $[0,\infty)^2$.

4.2. Persistence and the Role of Competition. We now explore the effects of competition in the autonomous system (98a) and (98b). There are 6 different competition coefficients and to reduce the number of different cases we focus on the special case below where $\beta_i, \gamma_i = 0$:

$$x_{n+1} = \alpha_1 y_n + \alpha_2 x_n, \tag{102}$$

$$y_{n+1} = \frac{bx_n}{1+c_1x_n+c_2y_n}. \tag{103}$$

If α_i define the natural survival rates s_i, then this system is complementary to (3a), (3b), (4a), and (4b) in the sense that in both of those systems $c_2 = 0$.

By the last two corollaries, all orbits of the rational system (102) and (103) in $[0,\infty)^2$ are uniformly bounded if $c_1 > 0$ and $\alpha_2 < 1$ and they converge to the origin if $\alpha_1 b + \alpha_2 < 1$. We now examine this rational system in more detail using its folding, namely, the second-order rational equation

$$x_{n+2} = ax_{n+1} + \frac{\sigma x_n}{1+Ax_{n+1}+Bx_n}, \tag{104}$$

where

$$a = \alpha_2,$$
$$\sigma = \alpha_1 b,$$
$$A = \frac{c_2}{\alpha_1}, \tag{105}$$
$$B = \frac{1}{\alpha_1}(\alpha_1 c_1 - \alpha_2 c_2).$$

See (45); y-component is given by (44) or calculated directly using (102) as

$$y_n = \frac{1}{\alpha_1}(x_{n+1} - \alpha_2 x_n). \tag{106}$$

With initial values x_0 and $x_1 = \alpha_1 y_0 + \alpha_2 x_0$ derived from $(x_0, y_0) \in [0,\infty)^2$, x-component of the orbits $\{(x_n, y_n)\}$ of the system is obtained by iterating (104). The equation in (106) is passive in the sense that after x-component of the orbit is generated by the core equation (104) y-component is derived from (106) without any further iterations. This observation also establishes the nontrivial fact that solutions of (104) that correspond to the orbits of the system in $[0,\infty)^2$ are nonnegative and well-defined even for $B < 0$.

If $\alpha_1 b + \alpha_2 < 1$, that is, $\sigma < 1 - a$, then zero is the only fixed point of (104). Corollary 21 establishes that, in this case, zero is globally asymptotically stable relative to $[0,\infty)$. On the other hand, when $\alpha_1 b + \alpha_2 > 1$, that is, $\sigma > 1 - a$, then 0 is no longer a stable fixed point of (104). By routine calculations, one can show that zero is a saddle point when $1-a < \sigma < 1+a$ and if $\sigma > 1 + a$ then zero is a repeller.

In addition, when $\sigma > 1 - a$ and $a = \alpha_2 < 1$, system (102) and (103) also has a fixed point in $(0,\infty)^2$ given by

$$\bar{x} = \frac{\sigma - (1-a)}{(1-a)(A+B)} = \frac{\alpha_1(\alpha_1 b + \alpha_2 - 1)}{(1-\alpha_2)[\alpha_1 c_1 + (1-\alpha_2)c_2]},$$
$$\bar{y} = \frac{(1-\alpha_2)}{\alpha_1}\bar{x}. \tag{107}$$

We note that $\bar{x}$ is also a positive fixed point of folding (104). Under certain conditions, $\bar{x}$ attracts all solutions of (104) with positive initial values, and it is thus a survival equilibrium. We state the following result from literature; see [38].

Lemma 22. *Let I be an open interval of real numbers and suppose that $f \in C(I^m, \mathbb{R})$ is nondecreasing in each coordinate. Let $\bar{x} \in I$ be a fixed point of the difference equation*

$$x_{n+1} = f(x_n, x_{n-1}, \ldots, x_{n-m+1}) \tag{108}$$

and assume that the function $h(t) = f(t,\ldots,t)$ satisfies the conditions

$$h(t) > t \quad if\ t < \bar{x},$$
$$h(t) < t \quad if\ t > \bar{x}, \tag{109}$$
$$t \in I.$$

Then I is an invariant interval of (108) and $\bar{x}$ attracts all solutions with initial values in I.

Theorem 23. *Let $a < 1 < a + \sigma$; that is, $\alpha_2 < 1 < \alpha_1 b + \alpha_2$. If the function*

$$f(u,v) = au + \frac{\sigma v}{Au + Bv + 1} \tag{110}$$

is nondecreasing in both arguments, then the fixed point $\bar{x}$ attracts all solutions of (104) with initial values in $(0,\infty)$.

Proof. If we let

$$h(t) = at + \frac{\sigma t}{1 + (A+B)t} \tag{111}$$

then the fixed point $\bar{x}$ is the solution of $h(t) = t$. For $t > 0$, we may write $h(t) = \phi(t)t$ where

$$\phi(t) = a + \frac{\sigma}{1+(A+B)t} \quad \text{with } \phi(\bar{x}) = \frac{h(\bar{x})}{\bar{x}} = 1. \tag{112}$$

Now,

$$\phi'(t) = -\frac{\sigma(A+B)}{(1+(A+B)t)^2} < 0 \tag{113}$$

for all $t > 0$, so $\phi(t)$ is strictly decreasing for all $t > 0$. Therefore,

$$t < \bar{x}$$
$$\text{implies that } h(t) = \phi(t)t > \phi(\bar{x})t = t,$$
$$t > \bar{x} \tag{114}$$
$$\text{implies that } h(t) = \phi(t)t < \phi(\bar{x})t = t.$$

The rest of the proof follows from Lemma 22. □

Note that

$$f_u = a - \frac{A\sigma v}{(Au+Bv+1)^2},$$
$$f_v = \frac{\sigma(Au+1)}{(Au+Bv+1)^2} > 0. \tag{115}$$

If $\alpha_1 b + \alpha_2 > 1$ and $c_2 = 0$ then $A = 0$, so $f_u, f_v > 0$. Therefore by Theorem 23 $\bar{x}$ is globally asymptotically stable. However, if $c_2 > 0$, then f_u may not be positive, so the results of Theorem 23 may not apply to this case. The next result shows that orbits of the system may converge to $\bar{x}$ if $c_2 > 0$ but not too large.

Theorem 24. *Let $c_1 > 0$ and let $a < 1 < a + \sigma$; that is, $\alpha_2 < 1 < \alpha_1 b + \alpha_2$. Then there exists $c > 0$ such that for $c_2 \in [0, c]$ the fixed point $\bar{x}$ of (104) is globally asymptotically stable relative to $(0,\infty)$.*

Proof. Since

$$f_u = a - \frac{A\sigma v}{(Au+Bv+1)^2}$$
$$= \frac{a(Au+Bv)^2 + 2Aau + a + (2aB - A\sigma)v}{(Au+Bv+1)^2} \tag{116}$$

to ensure that $f_u \geq 0$ it suffices for $2aB - A\sigma \geq 0$; that is,

$$2\alpha_2 (\alpha_1 c_1 - \alpha_2 c_2) - c_2 \alpha_1 b \geq 0 \tag{117}$$

which is equivalent to

$$c_2 \leq \frac{2\alpha_1 \alpha_2 c_1}{\alpha_1 b + 2\alpha_2^2} \doteq c \tag{118}$$

and the proof is complete. □

If c_2 is sufficiently large then f_u is not positive on $(0, \infty)$. Furthermore, $\overline{x}$ also becomes unstable for large enough c_2, which we establish next by examining the linearization of (104) around $\overline{x}$.

The characteristic equation associated with the linearization of (104) at $\overline{x}$ is given by

$$\lambda^2 - p\lambda - q = 0, \tag{119}$$

where

$$\begin{aligned} p &= f_u(\overline{x}, \overline{x}) = a - \frac{(1-a) A\overline{x}}{1 + (A+B)\overline{x}}, \\ q &= f_v(\overline{x}, \overline{x}) = \frac{\sigma - (1-a) B\overline{x}}{1 + (A+B)\overline{x}}. \end{aligned} \tag{120}$$

The roots of (119) are given by

$$\begin{aligned} \lambda_1 &= \frac{p - \sqrt{p^2 + 4q}}{2}, \\ \lambda_2 &= \frac{p + \sqrt{p^2 + 4q}}{2}. \end{aligned} \tag{121}$$

Since $f_v(u, v) > 0$ for all $u, v \in (0, \infty)$ it follows that $q > 0$ and both roots are real with $\lambda_1 < 0$ and $\lambda_2 > 0$. Furthermore, $\lambda_2 < 1$ if

$$\frac{p + \sqrt{p^2 + 4q}}{2} < 1 \quad \text{that is } q < 1 - p \tag{122}$$

which is equivalent to

$$2(1-a)(A+B)\overline{x} > \sigma - (1-a). \tag{123}$$

This inequality holds, since $\overline{x} > 0$ under our assumptions on the parameters. Therefore, $\lambda_2 < 1$. On the other hand, $\lambda_1 > -1$ if and only if

$$\frac{p - \sqrt{p^2 + 4q}}{2} > -1 \quad \text{that is } p + 1 > q \tag{124}$$

which is equivalent to

$$2(Aa + B)\overline{x} > \sigma - (1+a). \tag{125}$$

Note that when $(1-a) < \sigma < (1+a)$ this is trivially the case since $\overline{x} > 0$ under our assumptions on the parameters. Thus, $\overline{x}$ is locally asymptotically stable if $\sigma < 1 + a$.

Next, $\lambda_1 < -1$ if $\sigma > 1 + a$ and

$$2(Aa + B)\overline{x} < \sigma - (1+a). \tag{126}$$

We summarize the above results in the following lemma.

Lemma 25. *Let $a < 1 < a + \sigma$; that is, $\alpha_2 < 1 < \alpha_1 b + \alpha_2$. Then the fixed point $\overline{x}$ of (104) is*

(a) *locally asymptotically stable if and only if (125) holds. In particular, this is true if*

$$\begin{gathered} 1 - a < \sigma < 1 + a, \\ \text{that is } 1 - \alpha_2 < \alpha_1 b < 1 + \alpha_2. \end{gathered} \tag{127}$$

(b) *It is a saddle point if and only if (126) holds with $\sigma > 1 + a$; that is $\alpha_1 b > 1 + \alpha_2$.*

Inequality (126) implies a range for c_2 that we now determine. Let

$$k = \frac{\sigma - (1+a)}{\sigma - (1-a)} < 1. \tag{128}$$

Then $k \in (0, 1)$ if $\sigma > 1 + a$,

$$\begin{aligned} &2(Aa + B)\overline{x} < \sigma - (1+a) \Longrightarrow \\ &\frac{2(Aa + B)}{A + B} < \frac{\sigma - (1+a)}{\sigma - (1-a)} (1-a) = (1-a) k. \end{aligned} \tag{129}$$

Since

$$\begin{aligned} 2(Aa + B) &= \frac{2}{\alpha_1} (c_2 \alpha_2 + c_1 \alpha_1 - c_2 \alpha_2) = 2c_1, \\ A + B &= \frac{1}{\alpha_1} \left[c_1 \alpha_1 + (1 - \alpha_2) c_2 \right] \end{aligned} \tag{130}$$

(129) is equivalent to

$$\frac{2c_1 \alpha_1}{c_1 \alpha_1 + (1 - \alpha_2) c_2} < (1-a) k = (1 - \alpha_2) k. \tag{131}$$

From the above inequality we obtain

$$c_2 > \frac{\alpha_1 c_1 \left[2 - (1 - \alpha_2) k \right]}{(1 - \alpha_2)^2 k} \doteq \overline{c}. \tag{132}$$

Thus if $c_2 > \overline{c}$ then $\overline{x}$ is a saddle point and in particular the fixed point $(\overline{x}, \overline{y})$ is unstable. These observations lead to the following which may be compared with Theorem 24.

Corollary 26. *Assume that (99) holds for system (102) and (103) and $\alpha_2 < 1 < \alpha_1 b + \alpha_2$. Then the fixed point $(\overline{x}, \overline{y})$ is unstable if $c_2 > \overline{c}$.*

Our final result establishes that when $c_2 > 0$ is sufficiently large system (102) and (103) can have a prime period two orbit which occurs as $\overline{x}$ becomes unstable. Existence of periodic orbits is established via the folding in (104).

The difference equation in (104) has a positive prime period two solution if there exist real numbers $m, M > 0$ and $m \neq M$ such that

$$\begin{aligned} m &= f(M, m), \\ M &= f(m, M); \end{aligned} \tag{133}$$

that is,

$$m = aM + \frac{\sigma m}{AM + Bm + 1}, \quad M = am + \frac{\sigma M}{Am + BM + 1} \tag{134}$$

from which we get

$$(m - aM)(AM + Bm + 1) = \sigma m, \quad (M - am)(Am + BM + 1) = \sigma M; \tag{135}$$

that is,

$$AmM + Bm^2 + m - AaM^2 - aBMm - aM = \sigma m, \tag{136}$$

$$AmM + BM^2 + M - Aam^2 - aBMm - am = \sigma M. \tag{137}$$

Taking the difference of the right and left sides of (136) and (137) yields

$$\begin{aligned} & B\left(m^2 - M^2\right) + (m - M) - Aa\left(M^2 - m^2\right) \\ & \quad - (M - m) = \sigma(m - M), \\ & (B + Aa)(m - M)(m + M) \\ & \quad = (\sigma - (1 + a))(m - M). \end{aligned} \tag{138}$$

When $m \neq M$, we get

$$(B + Aa)(m + M) = \sigma - (1 + a) \tag{139}$$

and since the left side of the last equation is positive this implies that $\sigma - (1 + a) > 0$. Stated differently, if $\sigma - (1 + a) < 0$, then (104) cannot have a positive prime period two solution.

Similarly, taking the sum of the right and left sides of (136) and (137) yields

$$\begin{aligned} & 2AmM + B\left(m^2 + M^2\right) + (m + M) \\ & \quad - Aa\left(m^2 + M^2\right) - 2aBMm - a(m + M) \\ & = \sigma(m + M). \end{aligned} \tag{140}$$

Adding and subtracting $2(B - Aa)$ to and from the left hand side of the last expression in (140) yields

$$\begin{aligned} & 2(A - aB - B + Aa)Mm + (B - Aa)(m + M)^2 \\ & \quad = (\sigma - (1 - a))(m + M); \end{aligned} \tag{141}$$

that is,

$$\begin{aligned} & 2(1 + a)(A - B)Mm = (\sigma - (1 - a))(m + M) - (B \\ & \quad - Aa)(m + M)^2 = (m + M)(\sigma - (1 - a) \\ & \quad - (B - Aa)(m + M)) = (m + M)\Big(\sigma - (1 - a) \\ & \quad - \frac{(B - Aa)(\sigma - (1 + a))}{B + Aa}\Big) \\ & \quad = \frac{m + M}{Aa + B}\left[(B + Aa)(\sigma - (1 - a))\right. \\ & \quad \left. - (B - Aa)(\sigma - (1 + a))\right]. \end{aligned} \tag{142}$$

Simplifying the right hand side, it follows that

$$\begin{aligned} & (1 + a)(A - B)Mm \\ & \quad = \frac{\sigma - (1 + a)}{(Aa + B)^2}\left[Aa(\sigma - 1) + aB\right]. \end{aligned} \tag{143}$$

Now, since we are assuming that $\sigma - (1 + a) > 0$, then $\sigma - 1 > 0$, so the right side of (143) is positive, which implies that $A - B > 0$. Stated differently, if $A < B$, then (104) has no positive prime period two solution.

From (143) we get

$$Mm = \frac{[\sigma - (1 + a)][Aa(\sigma - 1) + aBc]}{(1 + a)(A - B)(Aa + B)^2} := Q \tag{144}$$

and let $m + M = P$, from which we obtain that $M = P - m$ and $m = P - M$. This means that

$$m(P - m) = Q, \quad M(P - M) = Q; \tag{145}$$

that is, m and M are the roots of the quadratic

$$S(t) = t^2 - Pt + Q, \tag{146}$$

where $P, Q > 0$ and

$$t_{\pm} = \frac{P \pm \sqrt{P^2 - 4Q}}{2}. \tag{147}$$

To ensure that m and M are real, the roots of $S(t)$ must be real, which is the case if and only if $P^2 - 4Q > 0$; that is,

$$\begin{aligned} & [\sigma - (1 + a)]\left[\sigma - (1 + a) - \frac{4(Aa(\sigma - 1) + aB)}{(1 + a)(A - B)}\right] \\ & \quad > 0. \end{aligned} \tag{148}$$

We summarize the above results as follows.

Theorem 27. *The second-order difference equation in (104) has a positive prime period two solution if and only if all of the following conditions are satisfied:*

(a) $\sigma - (1 + a) > 0$.
(b) $A - B > 0$.
(c) $(\sigma - (1 + a))[\sigma - (1 + a) - 4(Aa(\sigma - 1) + aB)/(1 + a)(A - B)] > 0$.

The next result shows that a solution of period two appears when $\overline{x}$ loses its stability.

Corollary 28. *The second-order difference equation in (104) has a positive prime period two solution if and only if $\overline{x}$ is a saddle point.*

Proof. Suppose $\overline{x}$ is a saddle point. Then, by Lemma 25(b), $2(Aa + B)\overline{x} < \sigma - (1 + a)$ from which we infer that $\sigma - (1 + a) > 0$.

Now $2(Aa + B)\overline{x} < \sigma - (1 + a)$ implies that

$$\frac{2(Aa + B)}{(1 - a)(A + B)}(\sigma - (1 - a)) < \sigma - (1 + a) \tag{149}$$

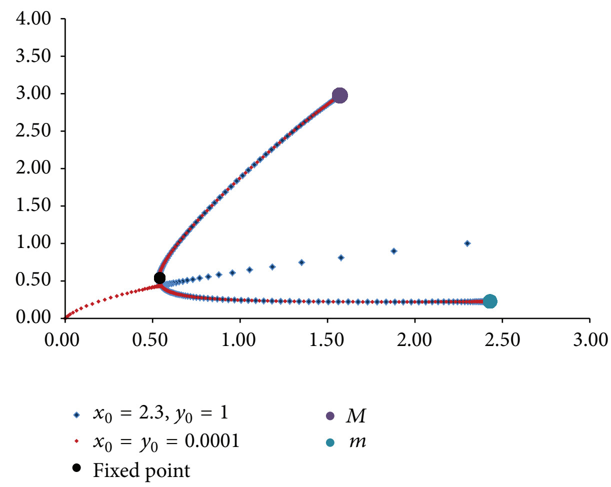

FIGURE 1: Orbits illustrating period two oscillations and the saddle point.

which is true if and only if

$$\begin{aligned} &2(Aa+B)(\sigma-(1-a)) \\ &\quad <(1-a)(A+B)(\sigma-(1+a)). \end{aligned} \tag{150}$$

Adding and subtracting $(1+a)(A-B)(\sigma-(1+a))$ to and from the right hand side of the last expression in (150) yields

$$\begin{aligned} &(1+a)(A-B)(\sigma-(1+a)) \\ &\quad +(\sigma-(1+a))((1-a)(A+B)-(1+a)(A-B)) \\ &=(1+a)(A-B)(\sigma-(1+a)) \\ &\quad +(\sigma-(1+a))(2B-2Aa). \end{aligned} \tag{151}$$

Therefore,

$$\begin{aligned} &2(Aa+B)(\sigma-(1-a))+2(Aa-B)(\sigma-(1+a)) \\ &\quad =4(Aa(\sigma-1)+aB) \\ &\quad <(1+a)(A-B)(\sigma-(1+a)); \end{aligned} \tag{152}$$

that is,

$$\begin{aligned} &(1+a)(A-B)(\sigma-(1+a))-4(Aa(\sigma-1)+aB) \\ &\quad >0 \end{aligned} \tag{153}$$

from which we infer that $A-B>0$ and the roots of $S(t)$ are guaranteed to be real and positive. This satisfies all the conditions of Theorem 27 which completes the proof. □

Corollary 29. *Assume that (99) holds and furthermore $\alpha_2 < 1 < \alpha_1 b+\alpha_2$ and $c_2 > \bar{c}$. Then system (102) and (103) has a cycle of period two in $(0,\infty)^2$.*

Figure 1 shows two orbits of system (102) and (103) from initial points $(x_0, y_0) = (2.3, 1)$ and $(x_0, y_0) = (0.0001, 0.0001)$. Although both orbits converge to the period two cycle, a shadow of the stable manifold of the fixed point is also seen in the initial segments of the two orbits. If the initial points start exactly on the stable manifold of $\overline{x}$ then the solutions converge to $\overline{x}$.

We studied the dynamics of a general planar system that includes many common stage-structured population models that evolve in discrete time. Our hypotheses regarding system (2a) and (2b) and its parameters are more general than what is typically assumed in population models with the aim of gaining a broader understanding of the mathematical properties of the system. The study in this paper is rigorous but incomplete and many issues remain. Generalizing the results in Section 4 to a level closer to that in Section 3 leads to a more comprehensive treatment of planar or two-stage, discrete population models. Among other things, this involves a consideration of systems involving the Ricker function where it is necessary to add the possibility of complex behavior. A resolution of these and related issues is left to future studies of system (2a) and (2b).

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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